

RESEARCH LETTER

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Key Points:

- We derive a mechanistic model yielding an export efficiency upper bound as a function of temperature
- The model captures the upper bound of several efficiency-temperature data sets
- The model is simple and mechanistically links export production with metabolic theory

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On the temperature dependence of oceanic export efficiency

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Abstract Quantifying the fraction of primary production exported from the euphotic layer (termed the export efficiency ef) is a complicated matter. Studies have suggested empirical relationships with temperature which offer attractive potential for parameterization. Here we develop what is arguably the simplest mechanistic model relating the two, using established thermodynamic dependencies for primary production and respiration. It results in a single-parameter curve that constrains the envelope of possible efficiencies, capturing the upper bounds of several ef - T data sets. The approach provides a useful theoretical constraint on this relationship and extracts the variability in ef due to temperature but does not idealize out the remaining variability which evinces the substantial complexity of the system in question.

1. Introduction

The export of organic carbon out of the upper ocean is an important component of the climate system, driving the “biological pump” which reduces the partial pressure of atmospheric carbon dioxide and fuels the ecosystems of the deep ocean and benthos [Archer *et al.*, 2000]. The efficiency with which limiting resources (usually nutrients) are exported, relative to local recycling, is often termed the ef ratio, here defined as the ratio of the sinking flux of particulate organic carbon across a defined depth horizon and the integrated primary production P_p above that horizon, e.g., Laws *et al.* [2000]. Eppley and Peterson [1979] identified a simple, empirical relationship between ef and integrated primary production, but it has been difficult to establish a clear theoretical basis for the controls on ef due to the myriad physical and biological processes at play [de la Rocha and Passow, 2007].

Laws *et al.* [2000] examined a relatively detailed numerical model of the planktonic ecosystem, which suggested that ef is shaped by P_p and mixed layer temperature T . A compilation of self-consistent observations of export efficiency ef along with local physical and biogeochemical factors, from the Joint Global Ocean Flux Study (JGOFS) Process Study data, supported this interpretation. Both model and data suggested an approximately linear, negative correlation between ef and mixed layer temperature, T , and that the temperature dependence of the ecosystem processes which shape export production provide a dominant control on ef . Indeed, the temperature variation explained far more of the variance in ef than P_p in that data set. A series of subsequent studies [e.g., Laws *et al.*, 2011; Henson *et al.*, 2011; Dunne *et al.*, 2005; Maiti *et al.*, 2013] have explored the validity and possible forms of temperature- ef relationships, and there has been a significant increase in the empirical data constraints over the past 15 years. The simple correspondence between ef and T of Laws *et al.* [2000] is not clearly supported with a much expanded data set. Consequently, recent models and interpretations of these data sets have not lead to a consistent, simple relationship between ef and T .

However, Laws *et al.* [2011] revisited the ef - T relationship from an empirical perspective, showing that the upper bound of ef declines as temperature increases. Here we consider this upper bound from a mechanistic perspective. At the heart of the temperature dependence in the Laws *et al.* [2000] model is the differential temperature sensitivity of phototrophic and heterotrophic metabolism [e.g., López-Urrutia *et al.*, 2006; Huntley and Lopez, 1992; Eppley, 1972] (clearly characterized by Rose and Caron [2007]). We develop a highly idealized framework which reflects this key element. We argue that while finding a simple relationship between ef and T will be confounded by many other factors in real systems, there is a predictable mechanistic relationship between the maximum export ratio, ef_{\max} and T which reflects situations where all other limitations and constraints (e.g., nutrients) are relaxed, analogous to the interpretation of the Eppley Curve [Eppley, 1972] (see Figure 1a). There the simple parameterization relates to the upper bound of growth rate: in any given

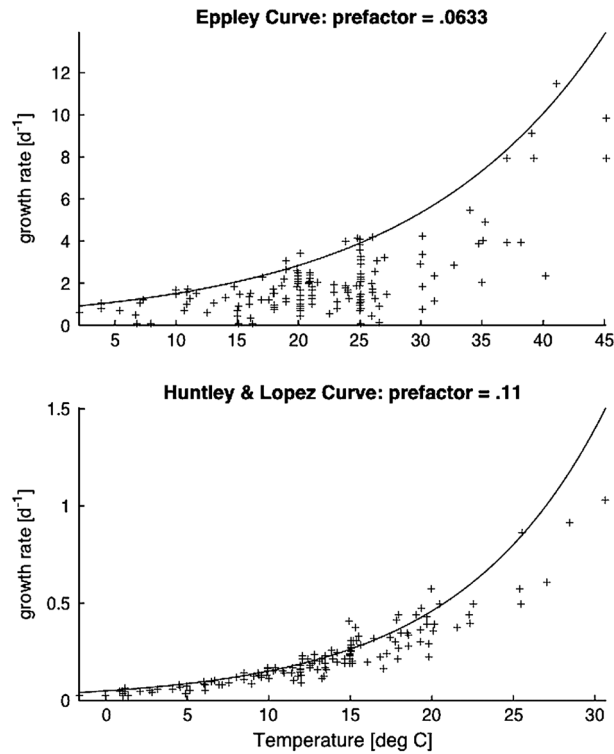


Figure 1. Temperature sensitivity for phytoplankton and copepod growth rates, adapted from (a) *Eppley* [1972] and (b) *Huntley and Lopez* [1992]. The temperature scaling prefactor is larger for the copepods, the key thermodynamic relation that drives this model. Another key difference is that copepod growth clusters along, while phytoplankton growth lies under, their respective curves; copepod growth appears to deviate significantly from this curve near $T = 24^\circ\text{C}$. These predictions from the above pictured original data sets have been additionally tested and verified in, e.g., *Rose and Caron* [2007]. Note the x axes of each subplot cover different limits. The prefactor is the value which multiplies temperature in the expressions $\mu \propto e^{0.063T}$, $\lambda \propto e^{-11T}$.

circumstance other factors such as nutrient limitation might restrict growth and so only the maximum of the observed data points represents the effect of temperature clearly.

Hence, we seek to characterize an envelope bounding export efficiency based on thermodynamic constraints. To do so, we will write the simplest model which captures the essential dynamics (section 2). Starting with an ordinary differential equation describing the time rate of change of autotrophic biomass, we derive a predicted curve for maximum export efficiency as a function of temperature. In section 3 we show that this simple, mechanistic model captures the trends in a compilation of empirical data with global coverage [*Laws et al.*, 2000; *Dunne et al.*, 2005; *Henson et al.*, 2011; *Buesseler and Boyd*, 2009] and discuss the value and limitations of the framework.

2. Methods: Model and Data

We first write a simple ordinary differential equation for the phytoplankton biomass density (p) in the upper ocean (the mixed layer, or euphotic zone, or above the thermocline):

$$\dot{p} = \mu p - \lambda p - \lambda' p - wp \quad (1)$$

where μ is a linear growth rate, λ represents loss due to grazing, and λ' represents losses from other processes including, e.g., viral lysis, senescence, and detrainment. w represents the rate of export as sinking particles; all coefficients have dimensions of inverse time. Assuming steady state and dividing through by μp , (1) becomes

$$0 = 1 - \left(\frac{\lambda + \lambda' + w}{\mu} \right) \quad (2)$$

Export efficiency is defined as the ratio of export production and primary production: $ef = wp/\mu p$ [Laws *et al.*, 2000], so (2) becomes

$$ef = 1 - \frac{\lambda + \lambda'}{\mu} \quad (3)$$

The key element of the model will be the differential temperature dependence of autotrophic and heterotrophic metabolism [Laws *et al.*, 2000]. We draw upon empirically established temperature dependencies for photosynthetic growth rates μ [Eppley, 1972; Rose and Caron, 2007] and zooplankton grazing rates λ [Huntley and Lopez, 1992; Rose and Caron, 2007] which are illustrated in Figure 1:

$$\lambda \propto e^{0.11T} \quad \mu \propto e^{0.063T} \quad (4)$$

Such temperature dependencies result from the different activation energies for photosynthesis and respiration, thus constrain growth thermodynamically [López-Urrutia *et al.*, 2006]. Loss processes represented by λ' may have their own temperature dependencies [e.g., Danovaro *et al.*, 2011]; we test for effects of possible λ' temperature dependence in section 3. After substituting these expressions for λ and μ into equation (3) the export ratio can now be expressed as

$$ef = 1 - \alpha e^{0.047T} - \lambda'/\mu \quad (5)$$

where α is a constant and λ'/μ represents reductions in ef due to loss processes other than grazing. The above expression highlights an important asymmetry; while there is only one way for biomass to increase, there are multiple pathways by which biomass p is lost. Thus, setting $\lambda' \equiv 0$ in equation (5) results in an expression for the upper bound on the export efficiency ratio when loss is comprised only of sinking and processes related to grazing. It is an upper bound because the copepod growth rates cluster around a compact curve in temperature space, and phytoplankton growth rates are spread *beneath* a maximum growth rate versus temperature [Huntley and Lopez, 1992; Eppley, 1972; Rose and Caron, 2007]. We note that the temperature scaling for autotrophic processes is valid up to 40°C, but the temperature dependency for zooplankton growth rate (thus grazing rate) is only a reasonable fit for up to 24°C, after which the temperature scaling breaks down and appears to flatten out, possibly indicative of a more complicated predator physiological response to temperature. This cutoff near 24°C is observable both in the original Huntley and Lopez [1992] paper and in the significantly expanded data of Rose and Caron [2007]: one possible hypothesis for this cutoff is that the decreased solubility of oxygen at higher temperatures begins to constrain heterotrophic processes, e.g., Deutsch *et al.* [2015].

There is no clear theoretical constraint with which to set α , so we may leave it as a parameter. To set α , we use one point from each data set described below, so that the remaining data can be used to test the prediction. We let α set the intercept, because $ef_{\max}(T = 0) = 1 - \alpha$. This is done by setting α so $ef_{\max}(T = 0)$ corresponds to the weighted average of the maxima of the data sets analyzed, leaving $\alpha = .24$. The formula used to compute α is

$$\alpha := 1 - \frac{1}{N} \sum_{i=1}^4 \frac{\max(ef)_i}{n_i}$$

where i is an index of each dataset used, N is the total number of data points, and n_i is the number of data points in each data set. The slope/curvature of the prediction itself is set by the temperature dependencies. In general, a larger α would correspond to a lower possible $ef_{\max}(T)$ for all values of T , with larger differences at lower temperatures. However, changing α by $\pm 10\%$ yielded no effect on the results described in the following section.

3. Results

In Figure 2 we compare the predicted upper bound on ef from equation (5) with four empirical data sets compiled from recent publications: Laws *et al.* [2000], Dunne *et al.* [2005], Henson *et al.* [2011], and additional data available from the Biological and Chemical Oceanography Data Management Office database [Buesseler, 2004]. The data sets are described in more detail in the cited sources; they include either sea surface or mixed layer temperature data, and export efficiency is evaluated using a variety of approaches, including estimates of export production based on carbon, oxygen, nitrate and other nutrients, and estimates of particle

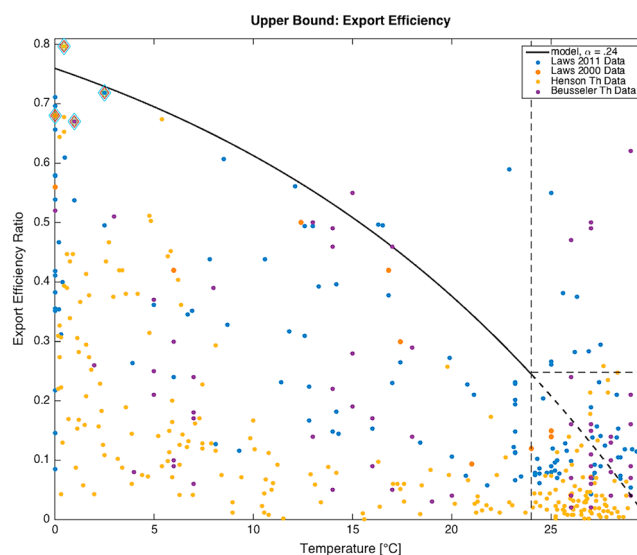


Figure 2. Model prediction for maximum export efficiency as a function of temperature, compared with data from sources described in Methods. The four points enclosed by diamonds were those taken to fix parameter $\alpha = .24$. The model agrees well with data in its applicable temperature range—vertical dashed line indicates the cutoff at 24°C observable in *Huntley and Lopez* [1992] and *Rose and Caron* [2007]. Remaining dashed lines indicate possible extrapolations of the model prediction above 24°C.

export based on sediment trap sinking fluxes or thorium isotopes. While the eclectic nature of the compilation introduces some comparative uncertainty, the number of data sources provides a large time window and global spatial coverage. Given the challenging nature of measuring and quantifying export, only recently has a sufficiently large body of data emerged with which to test such theories.

Over the temperature range for which the model is applicable, 0–24°C, the predicted upper bound and the maximum observed ef show very good agreement. There is only one significant outlier at 23°C, and the data points span the entirety of the domain beneath as expected. The spread reflects the influence of other loss processes (λ') that reduce ef , as well as constraints other than temperature on phytoplankton growth rates—i.e., the spread that underpins the Eppley μ -T relationship (see Figure 1 and equation (3)). Above 24°C the exponential extrapolation of the prediction does not capture the maximum extent of the empirical data. We attribute this to a breakdown of the exponential relationship between zooplankton growth rates and temperature above this threshold (Figure 1b). However, the mechanisms underlying that breakdown are not clear and may be the result of either metabolic or environmental constraints.

The variability in the distribution of the data in Figure 2 is indicative of the natural variability and complexity of carbon export and is likely due to a number of compounding effects, e.g., sampling difficulties [Buesseler *et al.*, 1994], growth intermittency, eddy subduction [Omand *et al.*, 2015], and the number of different remineralization pathways available to the community (i.e., in the λ' term) which this model ignores. Indeed, this complexity indicates the intractability of a simple mechanistic description of export, which suggests the utility of mechanistic approaches for establishing *constraints* rather than parameterizations.

Here our central hypothesis is that the difference in temperature dependencies of autotrophic and heterotrophic growth controls the envelope of variations in ef . This implies that the temperature dependence of the unresolved loss processes, λ' , is relatively weak. This assumption can be tested by rescaling all ef data points by the predicted ef_{\max} curve and asking if the distribution changes as temperature increases. If the mean \bar{ef} or normalized variance σ^2/\bar{ef} varies with temperature, this suggests λ' has some temperature dependence. In turn, this would demand to be incorporated into a relationship between ef and T . However, when all data is normalized by the $ef_{\max} = 1 - \alpha^{0.47T}$ curve, i.e., the predicted influence of temperature is removed, we see no change in \bar{ef} or σ^2/\bar{ef} with temperature. This demonstrates that the model captures all systematic temperature dependence in the data (Figure 3) and that the remaining variability is attributable to other factors.

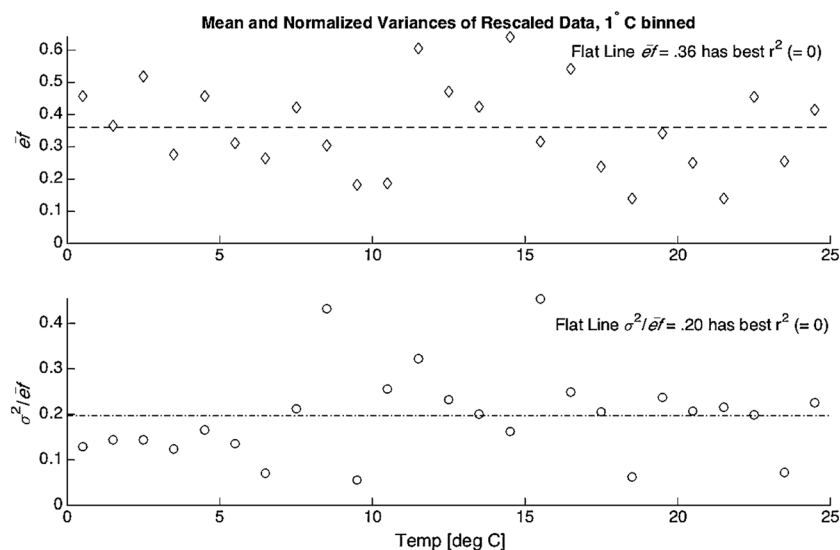


Figure 3. Mean and normalized variance of the data after being binned at width 1°C and rescaled by predicted maximum export efficiency. Binned values are best explained by a constant line; the best fit regression line computed with ordinary least squares has a negative adjusted r^2 ; thus, after the model's prediction for temperature dependence has been removed, no variation in the binned values can be explained by temperature.

4. Discussion

The model prediction described here shows good agreement with data, yielding an upper bound on potential export efficiency guided by thermodynamic constraints. This envelope, in the spirit of the Eppley curve, hinges on the asymmetry between the number of pathways for primary production (one) and loss (several). Despite the variety of methods used to estimate export efficiency from field data [Henson *et al.*, 2011] all data sets approach and fall within the upper bound suggested by the model.

Limitations of the model include the strong assumption of steady state. The implications of this could be examined in time-dependent models. The assumption is more applicable in regions where upper ocean phytoplankton biomass density is slowly varying and least applicable in bloom forming regions. Collecting further metabolic data for grazers growth rates above 24°C, and an exploration of the mechanisms controlling metabolism at warmer temperatures could improve the foundation of the model.

Using this model to extract the temperature dependence of ef provides a foundation for investigating dependencies of ef on other variables including primary productivity [e.g., Laws *et al.*, 2011; Maiti *et al.*, 2013], opening the door for further development of mechanistic models of ocean carbon export [e.g., Siegel *et al.*, 2014]. There is a longstanding history of relating primary production and export [Eppley and Peterson, 1979; Laws *et al.*, 2011], though the relationship may be complex and regionally varying [Maiti *et al.*, 2013]. Clearly, understanding and mechanistically modeling the relationship to primary production would be a valuable extension to this model [see Laws *et al.*, 2011]. An interesting avenue for extension of this model would be to incorporate an allometric component since cell size has been empirically related to export rates [Guidi *et al.*, 2009] and the theoretical foundations have been explored [e.g. Laws, 1975].

We show that this model describes all systematic temperature dependence of the ef data (Figure 3) and that this is due to the difference in temperature dependencies of autotrophic and heterotrophic metabolisms. A significant inference of the model is that independent of other factors, a warming ocean should lead to a weakened export efficiency and biological carbon pump, by a quantifiable extent. Of course this may not be the dominant factor since other, indirect effects of warming such as changes in stratification and primary productivity will also be at play.

In summary, we present a model that provides a mechanistic constraint on the range of potential export efficiency values, based on empirically established temperature dependencies and differential equation approaches fundamental to marine ecology. The prediction is quite general, reinforced by a collection of data sets and the simplicity of its derivation. While this approach moves away from predictions or

parameterizations which expect a tight relationship between export efficiency and temperature, it provides a potentially useful framework by linking metabolic theory and the biological carbon pump and acknowledges the substantial complexity of the flow of carbon in the upper ocean.

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